OBSERVATIONS IN THE SYSTEMATICS OF NEMATODES BELONGING TO THE GENUS SYPHACIA SEURAT, 1916

COLIN GERALD OGDEN

Pp. 253-280; 5 Plates, 39 Text-figures

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 20 No. 8

LONDON 1971

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), instituted in 1949, is issued in five series corresponding to the Departments of the Museum, and an Historical series.

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 a separate supplementary series of longer papers was instituted, numbered serially for each Department.

This paper is Vol. 20, No. 8 of the Zoological series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.

World List abbreviation Bull. Br. Mus. nat. Hist. (Zool.).

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TRUSTEES OF THE BRITISH MUSEUM (NATURAL HISTORY)

OBSERVATIONS IN THE SYSTEMATICS OF NEMATODES BELONGING TO THE GENUS

SYPHACIA SEURAT, 1916

By COLIN G. OGDEN

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SUMMARY

The genus Syphacia is reviewed and its subgeneric division suggested by Chabaud and Biocca (1955) is discussed. Methods for preparing fresh and preserved specimens for examination by the scanning electron microscope are compared. It is suggested that the structure of the head in Syphacia falls into four distinct patterns, and it would appear that this feature may be of value, as in other oxyurids, for delimiting groups of species. The structure of the head, cuticle and the male mamelon as seen by the scanning electron microscope are illustrated. The use of measurements for comparative studies in parasitic nematodes is discussed. Four species: S. obvelata, S. emilromani, S. stroma and S. muris are compared and the methods for expressing this data are reported. Eleven species of the genus are redescribed, and it is confirmed that S. obvelata and S. stroma are distinct species.

INTRODUCTION

Many of the descriptions of nematodes belonging to the genus *Syphacia* Seurat, 1916, appear to be inadequate by modern standards, with the result that difficulty may be

encountered in recognizing species which have been attributed to it. The writer became very aware of this difficulty when attempting specifically to determine some specimens of this genus recovered from the large intestine of the Lesser Bandicoot Rat, Bandicota bengalensis, in India. Owing to the abundance of both sexes in this material, the opportunity has been taken to study the morphological features found in these specimens and to compare them with similar features in specimens of Syphacia from various hosts already in the collections of the British Museum (Natural History). Use has also been made of the "Stereoscan" scanning electron microscope to elucidate certain structures which, although seen with the light microscope, are more accurately represented by the former instrument.

THE GENUS SYPHACIA

The genus Syphacia was erected by Seurat (1916) to accommodate two species formerly associated with the genus Oxyuris, namely, O. obvelata (Rudolphi, 1802)

and O. pallaryi Seurat, 1915.

Tiner (1948) in his review of the genus listed thirteen species, and suggested that S. stossichi (Setti, 1897) and S. trichosuri Johnston & Mawson, 1938, should be treated as Oxyuris (sensu lato) species. This treatment of these species has been accepted by Chabaud & Biocca (1955) and Skrjabin et al. (1960). One of the species listed by Tiner, namely, S. obubra Baylis, 1936, has since been designated as the type-species of the genus Syphaciurus Skrjabin & Schikhobalova, 1951. This opinion is based mainly on the unusual structure of the head of the female specimens and has been accepted by Chabaud & Biocca (1955), Yamaguti (1961) and Chabaud (1965). Khera modifies Tiner's (1948) differential key slightly and adds another species, S. tineri Khera, 1956.

Nineteen species of *Syphacia* are listed and described by Skrjabin, Schikhobalova and Lagodovskaya (1960), one of which, *S. montana* Yamaguti, 1943, was apparently overlooked by Tiner (1948), Chabaud & Biocca (1955) and Khera (1956) in their lists of species. Some comparative studies have been made by Kruidenier, Mehra & Harkema (1961) on the differences between *S. peromysci* and *S. samorodini*, previously considered to be synonymous by reviewing authors, however, they suggest that it

would be better at present to regard both species as distinct.

Division into subgenera

Chabaud & Biocca (1955) have used the number of mamelons in the males for dividing the genus into two subgenera, namely (Syphacia) possessing three mamelons and (Syphatineria) possessing two mamelons. The subgenus (Syphacia) automatically has S. obvelata as its type-species and these authors include ten other species:—S. arctica Tiner & Rausch, 1950; S. baylisi; S. frederici; S. muris; S. nigeriana Baylis, 1928; S. peromysci Harkema, 1936; S. ratti; S. stroma; S. thompsoni Price, 1928 and S. venteli. According to Chabaud & Biocca the second subgenus (Syphatineria) has S. pallaryi as its type-species, and includes six other species:—S. citelli Tiner & Rausch, 1950; S. eutamii Tiner, 1948; S. paraxeri Sandground, 1933; S. pearsei Baylis, 1928; S. sciuri Mirza & Singh, 1934 and S. transafricana Chabaud & Biocca, 1955. The total number of species attributed to the

genus by Chabaud and Biocca is therefore eighteen. They also observed that the species appear to be divided on the basis of the family to which the host belonged in the Order Rodentia. Those species with hosts attributed to murine rodents being in the subgenus (*Syphacia*), whilst those with hosts in sciurine rodents being in the subgenus (*Syphatineria*).

The division of Syphacia into two subgenera is accepted by Skrjabin, Schikhobalova & Lagodoskaya (1960), who list three additional species, S. lahorea Akhtar, 1955; S. tineri Khera, 1954 and S. montana Yamaguti, 1943, belonging to the subgenus (Syphacia). The Russian authors' classification seems to disregard Chabaud & Biocca's subgeneric division on biological grounds, because S. (Syphacia) lahorea occurs in a sciurid in addition to the transference of S. sciuri to (Syphacia).

Recently, twelve additional species have been ascribed to the genus, namely: S. (Syphacia) emilromani Chabaud, Rausch & Desset, 1963; S. srivastavi Sinha, 1957; S. (Syphatineria) tjanschani Ablassov, 1962; S. (Syphatineria) toschevi Petrow & Bayanov, 1962; S. (Syphacia) coli Schmidt & Kuntz, 1968; S. (Syphacia) magnispiculata Schmidt & Kuntz, 1968; S. (Syphacia) critesi Schmidt & Kuntz, 1968; S. (Syphacia) oceanica Schmidt & Kuntz, 1968; S. (Syphacia) lophuromyos Quentin, 1966; S. (Syphacia) megaloon Quentin, 1966 and S. (Syphacia) alata Quentin, 1968. Nevertheless, S. srivastavi must be treated as a doubtful species because it was described (Sinha, 1957 & 1960) from female specimens found in the stomach of the domestic pig, whereas the normal location of Syphacia species is the large intestine or caecum of rodents. The description and figures, particularly that of the head, do not appear to agree with the diagnosis of the genus Syphacia.

SCANNING ELECTRON MICROSCOPY

Live specimens of Syphacia stroma were collected from the intestine and caecum of Apodemus flavicollis, captured in the New Forest, Hampshire, England. Two methods of preparing these specimens for examination by the scanning electron microscope have been tried. In the first method the animals were washed several times with distilled water, then with a minimum of water they were frozen to -20° C, transferred to a freeze-drying unit and reduced to -50° C (Harris, 1968); in the second method they were fixed in 4% glutaraldehyde in 0·1 M cacodylic acid buffer, washed several times in the buffer followed by several washes in distilled water and freeze-dried as above. This latter method appears to produce the best results, because the body-cuticle is clean, whereas with the first method the body-cuticle is overlaid with mucus.

Preserved specimens of all the species dealt with in this report, with the exception of *S. pearsei*, have been examined, although in five cases it has only been possible to examine female specimens. The preserved specimens are transferred from either 4% formalin or 80% alcohol in a series of gradual dilutions to distilled water. It appears from specimens examined that formalin fixation is preferable to alcohol fixation. Unfortunately, the original fixative used in all cases is unknown and no conclusive result can be drawn in this instance. The distilled water used in all the methods outlined above is triple-glass distilled.

The reason for using the scanning electron microscope in the examination of these

species is that it is often difficult to interpret light-microscope studies of en face preparations and adequately to present the results. This microscope has assisted in both these respects, as it is now possible to examine whole specimens to a higher magnification and to illustrate them. The main difficulty encountered in the examination of en face features with the present material is that the lip-structure of those preserved specimens having large lip lobes has collapsed or distorted on freezedrying, as a consequence the en face micrographs of S. obvelata and S. muris are not included in this report. The structure of the cuticle is not discussed in detail, because of the uncertainty of interpreting the structures seen. Nevertheless, it would appear that in some species the cuticle is smooth, whilst in others there are small longitudinal ridges additional to the normal transverse striations (compare Pl. 5, figs. A & C). On the cuticle of female specimens of one species, S. transafricana, bacteria are seen lying in the transverse ridges (Pl. 5, fig. C). An additional feature of the male mamelons of the five species examined is the presence of small papillalike structures, which appear to be arranged in lines between the annulations. Examination of the cloacal region of male specimens in the present material has not been successful.

GENERAL MORPHOLOGY

The cuticle is marked with distinct transverse striations. Narrow lateral alae commence at the anterior end of the body and terminate slightly anterior to the level of the anus; they are present in both sexes. The cuticle in the cephalic region is often inflated to form a cephalic vesicle, and cervical alae are sometimes present.

The oesophagus is characterised by a small, unmodified pharyngeal portion, followed by the usual club-like corpus which is constricted prior to the oesophageal bulb. The triradiate valvular apparatus of the posterior bulb is typical of oxyurids. The anterior half of the oesophagus is modified by the folding of the oesophastome, to give the appearance of tooth-like structures. These structures are described by Yamaguti (1943) as a specific character of *S. montana*. Nevertheless, this feature is present in all of the specimens examined.

The nerve ring is situated approximately at the middle of the oesophagus. Ramisz (1965) has described the nervous system of *S. obvelata*. The excretory pore is usually found posterior to the oesophageal bulb, but anterior to the vulva in the female. Both of these characters are sometimes difficult to find. The tail in both sexes

narrows to a sharp point.

Male. The posterior end of the body is usually curved ventrally. The cuticle is characterised by the presence of two or three bosses with distinct transverse ridges, referred to as mamelons, situated on the ventral surface, approximately between the middle of the body and the cloacal opening. Each ridge on the mamelons is split along its transverse axis into two shallow elevations, between which lie small papillalike structures (Pl. 4, fig. D). There is no distinct pattern in the distribution of the mamelons on the body, although they give the appearance of being equally spaced, this, however, is not the case. The size and structure of the mamelons appears to depend to a large extent on the age of the specimen and the degree of ventral curving to the posterior end of the body, the latter feature causes the annules of the cuticle

to become compacted and the mamelon to protrude from the normal body line. This is easily seen in specimens recovered in sufficient numbers from one host, where the variation of ventral curving can range from only slight to perhaps two complete coils. The mamelons are usually recognizable macroscopically, but occasionally it is necessary to examine the specimens ventrally to see the most anterior mamelon. The cuticle around the cloacal opening is inflated slightly to form small caudal or bursal alae which extend from the most anterior pair of pre-cloacal papillae to the post-cloacal papillae. There are three pairs of caudal papillae, a medium-sized pair just anterior to the cloacal opening, a smaller pair level with the cloacal opening and a large pair posterior to the cloacal opening. There is a single spicule, which is pointed distally, and a complex gubernaculum.

Female. The vulva is situated in the anterior third of the body, behind the level of the oesophageal bulb. It is slightly protruded in some specimens and occasionally has a dark brown cap covering the tip (Pl. 3, fig. F). The vagina is short and the musculature of the ovijector is well developed. The uterus is single, usually filling the body-cavity posteriorly and sometimes extending anteriorly beyond the vulva. The eggs are usually flat on one side and smoothly curved on the other.

Structure of the head

The following features are common to all the species studied. The mouth opening is small and circular, leading into a shallow buccal cavity. The head bears three lips of equal size, two sub-ventral and one dorsal, with the cephalic papillae and amphids situated slightly posterior to them. The four single cephalic papillae are dorso-and ventrolateral in position, whilst the lateral amphids are slightly anterior to their level. In addition, an inner circle of six circumoral papillae is present in some species (see fig. 4).

There appear to be four distinct patterns in the form of the head. The first is represented in three species, S. citelli, S. pallaryi and S. transafricana, in which the lips are reduced in size (fig. 6) and have a cuticular thickening giving then a distinct triangular shape (Pl. 2, fig. B). The second is found in five species, S. obvelata, S. emilromani, S. stroma, S. peromysci and S. muris, all having pronounced lip-lobes (fig. 5, Pl. 1, figs. A & C) and occasionally an inner thickening of the cuticle to form a toothlike structure. The third is found in only two species, S. pearsei and S. thompsoni, in which the lip-lobes are separated from each other. The space between the lips extends to form interlabial grooves (fig. 7, Pl. 1, fig. E), which are similar to those described as either "labial grooves" in some Ascarid species or "cervical cordons" in the Heterakidae. The fourth pattern is represented only in S. eutamii. In this species the lips are supported by individual cuticular processes from the buccal cavity, with a supporting septum connecting it to the apical region of each lip (Pl. 3, fig. B). Individual variations of these four patterns are reported later under the species description.

COMPARATIVE MEASUREMENTS

The presentation of measurements in comparing species of this genus can be misleading, because of the similarity in the overall size of these animals. For example,

there are eight species with three mamelons in which the body-size of the male lies between one and two millimetres. The usual methods of presenting measurements of nematodes are confined to four approaches; ratios; graphically; individual animal measurements; and the mean value of a series of measurements.

If the ratios normally used in describing free-living nematodes are applied to

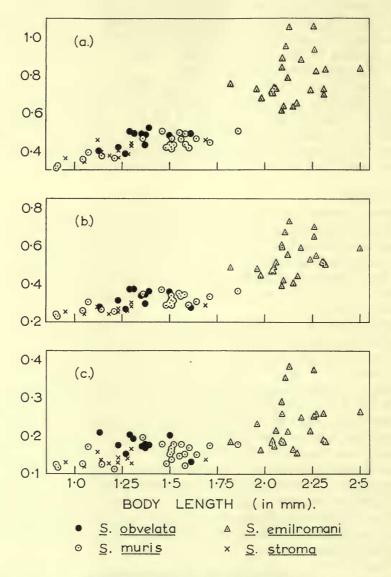


Fig. 1. Distance of mamelons from cloacal opening of male, vertical scale; plotted against the total body length, horizontal scale (all measurements in mm): (a) anterior mamelon (b) middle mamelon (c) posterior mamelon.

parasitic nematodes the limitation of each species will depend on the number of specimens found infesting the host-animal, or in a series of similar hosts collected in the same locality at the same time. That preservation can have a marked effect on such ratios has been pointed out by Inglis (1957), who considers that "V" appears to be the ratio least likely to show the effects of preservation, agreeing in part with Taylor & Jenkins (1957). In summarising the use of these ratios, with reference to their use in comparing parasitic nematodes, Inglis concludes that ratio "a" is unreliable. Regarding ratio "c", he considers that it may be particularly sensitive to variation in the length of the body when the tail of a species is narrow and in the form of a cuticular spike.

Only Roman (1951), of those authors who have used measurements for comparative purposes in the genus *Syphacia*, has used a graphical approach by means of "polygones de frequence". Some authors have listed individual measurements, but most have restricted their observations to listing only the range and mean of each of the characters used. For example, Hussey (1957), Kruidenier et al. (1961) and Bernard (1963) all give tables of measurements.

The species used in this present comparison of measurements, S. obvelata, S. emilromani, S. stroma and S. muris have been recovered from Clethrionomys glareolus Apodemus sylvaticus argenteus, Apodemus s. sylvaticus and Bandicota bengalensis, respectively. The specimens of S. obvelata, eleven males to approximately one hundred and twenty females, are from the caecum of three hosts caught in Witham Woods, near Oxford. Those of S. emilromani are from the intestine of one host from North Honschu, Japan, and those of S. stroma are from one host from Bagley Wood, near Oxford, both of these infestations are large, but they are represented by a proportion of roughly I: Io males to females. The specimens of S. muris, twenty-two males to approximately sixty females, are from the large intestine of two hosts, caught in Calcutta, India, and are unusual in the proportion of male to female specimens being small. All male specimens have been measured, with the exception of S. emilromani, where an arbitary number of twenty-five has been taken. Further twenty-five female specimens taken at random from each species have also been measured.

The individual measurement for each character in this study has been taken at the same position, or as near as possible, in each specimen. The measurement for the male mamelon is the distance between the middle of each mamelon and the cloacal opening. In the male, the body-breadth has been taken at a point just anterior to the foremost mamelon, whereas in the female it has been taken just posterior to the vulva. A maximum of three eggs, selected at random, from each gravid female have been measured. The range of measurements for the species are given in Table 2, the figures in brackets being the mean values.

Using the mean values as a comparison of the measurements given in Table 2a, the values obtained from the males of S. obvelata and S. stroma appear to be in close agreement, while S. emilromani appears to be larger than these two species in all dimensions, except in the length of the spicule and the gubernaculum, and S. muris differs in the size of the spicule, gubernaculum and tail from the other three species. A similar comparison of the females, Table 2b, shows that S. obvelata appears to differ

in the length of the tail from the other three species and in the position of the vulva from S. muris and S. emilromani; S. stroma appears to have the smallest tail, but the position of the vulva is similar to S. obvelata; S. emilromani differs from the other species in the length of its oesophagus. In size, the eggs of S. emilromani and S. muris

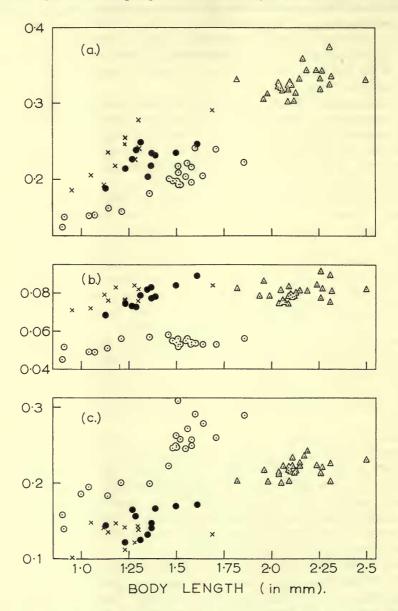


Fig. 2. Comparison of males: (a) length of oesophagus (b) length of spicule (c) length of tail, vertical scales; plotted against the total body length, horizontal scale (all measurements in mm). Symbols for each species are given in Fig. 1.

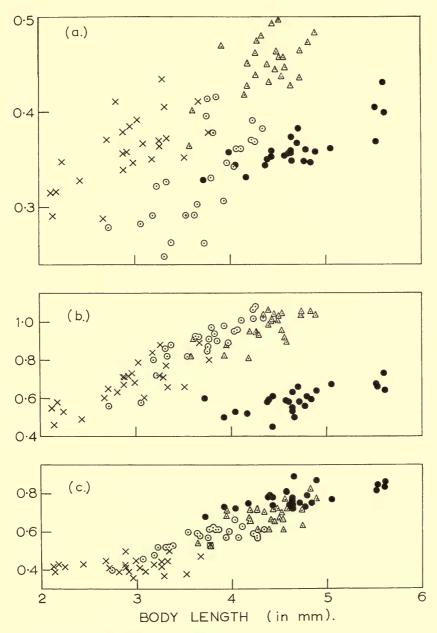


Fig. 3. Comparison of females: (a) length of oesophagus (b) distance of vulva from anterior end of body (c) length of tail, vertical scales; plotted against the total body length, horizontal scale (all measurements in mm). Symbols for each species are given in Fig. 1.

are similar, but differ from those of S. obvelata and S. stroma, the latter, the smallest

species, having the largest eggs.

By expressing these results graphically it is possible to examine the distribution of the individual measurements. To determine the value of the position of the mamelons on the males as a specific character, the distance of each mamelon from the cloacal opening is plotted against the body-length (fig. 1). The distance from the cloacal opening being used in preference to the distance from the posterior end of the body, in an attempt to eliminate any variation due to the species in the length of the tail. It is evident from the scatter of this data that the position of these structures is not suitable for use as a specific character, in fact the scatter might suggest that the structures are uniformly distributed.

It appears (fig. 2) that the correct assumptions have been assessed from the tables of measurements of male specimens, S. muris being distinct in the size of the spicule and tail. The size of the spicule is plotted (fig. 2 (b)) to show that there is no apparent effect of body size on this feature. The females (fig. 3), appear to fall into two groups on the basis of the length of the oesophagus, S. stroma and S. emilromani having the longer, with S. muris and S. obvelata the shorter oesophagus. Only S. obvelata differs from the others in the position of the vulva, and there is no apparent difference between any of the species in the length of the tail. These results are in some ways contrary to the conclusions drawn from the tables of measurements discussed above.

The results expressed as ratios, together with the standard deviation and range of values are shown in Table I. Considering the males first, there appear to be differences in ratio "b" between all four species. The difference in ratio "c" between S. muris and the other species is considered to be distinct. The female specimens appear to fall into two groups using ratio "b": (i) S. obvelata and S. muris; and (ii) S. emilromani and S. stroma. Ratio "c" appears to be similar for all four species, although the variation exhibited in the range of values for S. stroma cannot be explained. The difference in ratio "V", shows that S. obvelata can easily be differentiated from the other three species.

To summarise the results of the present comparison of measurements: the males of S. muris can be differentiated from the other three species by the size of the spicule, gubernaculum and tail; the males of S. emilromani are larger in body-length than the other three species, but there is no apparent difference between S. obvelata and S. stroma; the females of S. obvelata are distinct in the position of the vulva, and those of S. stroma in the size of the eggs; it also appears that the females of S. obvelata and S. muris differ in the size of the oesophagus from S. stroma and S. emilromani.

The conclusions that can be drawn from the methods used are that expressing the results as mean values is unsatisfactory for comparative purposes and preference must be given to the use of graphs or ratios. This is certainly the case when the infestation contains numerous specimens. In those instances where the infectation is numerically poor, it seems imperative to quote individual measurements to enable future comparisons of this nature to be made.

DESCRIPTION OF SPECIES

Syphacia obvelata (Rudolphi, 1802)

- S. artica Tiner & Rausch, 1950
- S. montana Yamaguti, 1943
- S. nigeriana Baylis, 1928

MATERIAL STUDIED. II 33, 25 9 ex caecum *Clethrionomys glareolus*. Witham Wood, Oxford. B.M. (N.H.) Reg. Nos. 1966.329–378.

13, 599 ex intestine Microtus agrestris neglectus. Loch Tay, Perthshire.

B.M. (N.H.) Reg. Nos. 1964.1697-1715.

533, 25♀♀ ex Clethrionomys rufocanus bedfordiae. Rebun Island, Hokkaido, Japan.

333, 10♀♀ ex intestine Taterillus gracilis angelus, Taterona kempi, Praomys tullbergi, Mastomys erythroleucus and (?) Lemniscomys striatus. Nigeria. Co-types & Paratypes of S. nigeriana. B.M. (N.H.) Reg. Nos. 1929.1.24.25–44.

 $2 \stackrel{?}{\circ} \stackrel{?}{\circ}$, $5 \stackrel{?}{\circ} \stackrel{?}{\circ}$ ex hind-gut *Mus dubius*. Colombo, Ceylon. B.M. (N.H.) Reg. Nos.

1935.9.12.51-75.

13, 5 \circlearrowleft ex caecum 'water-voles'. Salop, Perthshire. B.M. (N.H.) Reg. Nos. 1935.6.4.142–153.

MEASUREMENTS (in mm) See Table 2.

The cuticle is transversely striated and has small longitudinal ridges, similar to those occurring in *S. eutamii* (see Pl. 5, fig. A). The anterior end of the body has small cervical alae, which arise anteriorly and terminate at approximately the level of the oesophageal bulb. The head bears three prominent lip-lobes (fig. 5).

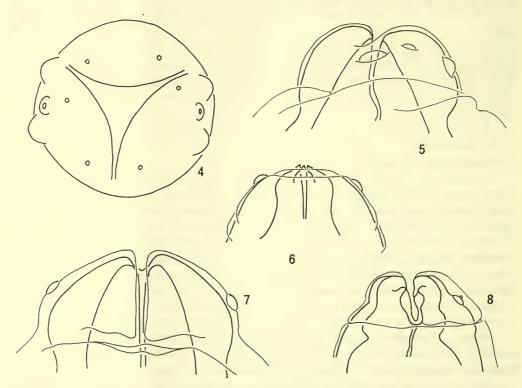
Male. The three mamelons have six or seven small papilla-like structures lying between their striations (Pl. 4, fig. D); the pre-cloacal and smaller cloacal papillae lie close together, whilst the post-cloacal pair are pronounced (figs. 9 & 13); the single spicule narrows slightly at approximately one-third of its total length from the proximal end and terminates distally in a sharp point (figs. 23 & Pl. 3, fig. E); the gubernaculum is complex (fig. 15); the tail tapers evenly to a fine point.

Female. The vagina normally runs posteriorly, but in some specimens, in which the uteri are packed with eggs, it is bent anteriorly; the lips of the vulva are protruded in some specimens; the eggs are of medium size (fig. 19 and Table 2b).

Discussion. It is impossible to recognise S. obvelata from its original description (Rudolphi, 1802) based on specimens from Mus musculus, or from the later description (Rudolphi, 1809) which was based on material from two hosts. This species has since been described by numerous authors, but the available information is still insufficient to differentiate it from other members of the genus, so that, two species, namely S. obvelata and S. stroma, have been reported to occur in the same host. It is now generally accepted, however, that S. obvelata is parasitic in the house-mouse, the bank-vole and the field-vole, whilst S. stroma is parasitic in the field mouse. Unfortunately, the collections of the British Museum (Natural History) have male specimens only from voles, but these appear to be sufficiently different from those from field-mice to enable them to be accepted as being specimens of S. obvelata.

The uncertainty of the specific characters of S. obvelata has led to the description

of several new species with slightly differing characters. The validity of these species is therefore difficult to determine, unless a direct comparison with specimens of $S.\ obvelata$ is undertaken at the same time. None of the authors seem to have done this, although they all compare their species with descriptions of $S.\ obvelata$. For example, Yamaguti (1943) describes $S.\ montana$ as differing from $S.\ obvelata$ in the length of the oesophagus and the accessory piece (= gubernaculum). Similarly, Baylis (1928) differentiates $S.\ nigeriana$ from $S.\ obvelata$ thus "... notably in the much greater length of the tail in the female, and in other minor points", whilst Tiner & Rausch (1950) could not differentiate the males of $S.\ obvelata$, $S.\ nigeriana$,



Figs. 4-8. 4. En face view of head, S. stroma 5. Dorsal view of head, S. obvelata. 6. Dorsal view of head, S. pallaryi. 7. Dorso-lateral view of head, S. thompsoni.

8. Dorso-lateral view of head, S. pearsei.

S. venteli and S. muris from their species, S. arctica, but considered the size of the eggs and the length of the female tail sufficiently different to warrant the erection of a new species.

A comparison of the measurements of specimens of Syphacia from Clethrionomys glareolus and C. ruficanus, the latter being the type-host of S. montana (see Chabaud et al. 1963), are shown in Tables 2 & 3. The agreement between the two sets of measurements is close. In addition, using the ratios: b 6.38 \pm 0.81; c 8.79 \pm 0.73 males and b 12.63 \pm 0.95; c 5.60 \pm 0.34; V 14.7 \pm 1.44 females, the comparison

with those for *S. obvelata* Table I is good. The morphological characters of the two sets of specimens are also closely comparable, and accordingly *S. montana* is here treated as a synonym of *S. obvelata*.

The length of the female tail does not appear to be a specific character in the group of species examined earlier in this report, and although the eggs of *S. arctica* are slightly smaller than any the writer has seen in *S. obvelata* it is not considered that this character alone is sufficient to warrant a separate species. It is therefore suggested that *S. arctica* be treated as a synonym of *S. obvelata*.

The type-specimens of *S. nigeriana* have been re-examined, and they appear to be conspecific with *S. obvelata*. This is in agreement with the observation made by Bernard (1963) from a study of *Syphacia* specimens from *Gerbillus campestris* and *Mus musculus* in Algiers.

S. obvelata appears to be distinct principally in the structure of the head: in the male, the size and shape of the spicule and gubernaculum, in the pronounced post-cloacal papillae, in the length of the tail and the number and form of the mamelons; in the female, the length of the oesophagus, in the position of the vulva and in the size of the eggs.

Syphacia emilromani Chabaud, Rausch & Desset, 1963

MATERIAL STUDIED. 25 ♂♂, 25 ♀♀ ex Apodemus sylvaticus argenteus. Mt. Hakkoda, North Honschu, Japan. Paratype specimens.

MEASUREMENTS (in mm) See Table 2.

The head bears three prominent lip-lobes (Pl. 3, figs. C & D).

Male. There are three mamelons on the ventral surface of the cuticle; the precloacal and cloacal papillae lie close together and the postcloacal pair are not pronounced; the spicule (fig. 24) is similar to those of S. obvelata and S. stroma; the gubernaculum is also similar in general appearance to that of S. obvelata, but differs in having a series of notches on the distal barb-like structure (fig. 16); the tail tapers evenly to a point.

Female. The vagina runs posteriorly from the vulva in all the specimens examined; the eggs are small (fig. 20).

DISCUSSION. This species is considered by Chabaud et al. (1963)* to differ from the known species of the genus in the absence of oesophageal "teeth", in the position of the four cephalic papillae and the size of the eggs.

S. emilromani appears to be similar to S. stroma in many characters, including the structure of the head, but differs from it in the size of the body, the shape of the gubernaculum and the size of the eggs. It is also similar to S. peromysci and S. samorodini in the shape of the gubernaculum and in the size of the eggs. These species are, however, much smaller than S. emilromani.

S. emilromani is distinct in the structure of the head and in the size of the body: the male in the number of mamelons, in the small post-cloacal papillae, in the shape

^{*} Note that in this (1963) description there is a typographical error, the length of the spicule being given as 195μ instead of 95μ .

of the gubernaculum and in the length of the tail; the female in the length of the oesophagus, in the position of the vulva and in the size of the eggs.

Syphacia stroma (Linstow, 1884)

Oxyuris stroma Linstow, 1884

MATERIAL STUDIED. 11 ♂, 25 ♀♀ ex intestine *Apodemus sylvaticus*. Bagley Wood, Oxford. B.M. (N.H.) Reg. Nos. 1926.4.20.126–145.

 $3 \ 3 \ 3, 4 \ 9 \ (immature)$ ex intestine *Apodemus sylvaticus*. Selsdon Woods, Surrey.

B.M. (N.H.) Reg. Nos. 1934.7.19.10-15.

533, 699 ex intestine *Apodemus sylvaticus*. Carmarthenshire. B. M. (N.H.) Reg. Nos. 1956.8.16.3-6.

8 \$ \$ \$, 12 \$ \$ ex intestine Apodemus flavicollis. Brockenhurst, New Forest, Hamp-

shire. B.M. (N.H.) Reg. Nos. 1970. 63-68.

533, 1099 ex intestine *Apodemus sylvaticus*. New Forest, Hampshire. B.M. (N.H.) Reg. Nos. 1970. 55–62.

 $5 \circ \circ$ ex intestine *Apodemus sylvaticus*. Charrade, France. B.M. (N.H.) Reg. Nos.

1935.11.6.190-193.

 $5 \circ \circ \text{ex}$ Apodemus hebridensis. Isle of Lewis, Hebrides. B.M. (N.H.) Reg. Nos. 1934.4.24.49–55.

MEASUREMENTS (in mm) See Table 2.

The head bears three prominent lip-lobes (Pl. 1, figs. A. B.). Cervical alae appear

to be absent. An inner ring of six circumoral papillae is present (fig. 4).

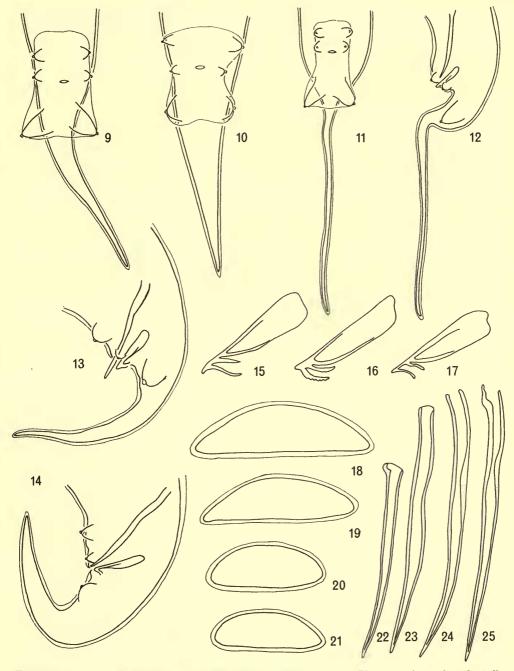
Male. There are three mamelons; between the transverse striations of each mamelon there are small papilla-like structures usually arranged in rows of five (Pl. 4, figs. B & E); the post-cloacal papillae are not pronounced (fig. 10 & 14); the spicule (fig. 25) and gubernaculum appear to be identical with those of S. obvelata; and the tail tapers gradually to a fine point (fig. 10).

Female. The body-length in these specimens is the smallest of those examined,

whereas the eggs are the largest (see Table 2b & fig. 18).

Discussion. This species was first described by Linstow (1884), who considered that the female specimens differed from those of S. obvelata in the position of the vulva and in the size of the eggs. Later, Seurat (1915 & 1916) considered S. stroma to be a synonym of S. obvelata. Morgan (1932) showed that male specimens of these two species could be separated by the differences in the structure of the post-cloacal papillae and by the thickness of tail. Nevertheless, Baylis (1936) pointed out that difficulties still existed between these species, because Morgan (1932) did not compare female specimens. Roman (1951) describes this species and distinguishes it from S. obvelata in the length of the oesophagus, in the structure of the head and in the position of the mamelons. These authors, Linstow, Morgan and Roman, appear to be justified in some of these conclusions, but they individually failed to give a complete diagnosis of the specific characters.

Syphacia stroma is here considered to be distinct in the structure of the head; the male in the number and structure of the mamelons, in the size of the post-cloacal



Figs. 9-25. 9. Ventral view of male tail, S. obvelata. 10. Ventral view of male tail, S. stroma. 11. Ventral view of male tail, S. muris. 12. Lateral view of male tail, S. muris. 13. Lateral view of male tail, S. obvelata. 14. Lateral view of male tail, S. stroma. 15. Lateral view of gubernaculum, S. obvelata. 16. Lateral view of gubernaculum, S. emilromani. 17. Lateral view of gubernaculum, S. muris. 18. Egg of S. stroma. 19. Egg of S. obvelata. 20. Egg of S. emilromani. 21. Egg of S. muris. 22. Lateral view of spicule, S. muris. 23. Lateral view of spicule, S. obvelata. 24. Lateral view of spicule, S. emilromani. 25. Lateral view of spicule, S. stroma.

papillae and in the length of the tail; the female in the length of the oesophagus, in the position of the vulva and in the size of the eggs.

Syphacia muris (Yamaguti, 1935)

Enterobius muris Yamaguti, 1935 Syphacia baylisi Maplestone & Bhaduri, 1942 Syphacia ratti Roman, 1945 Syphacia venteli Travassos, 1937

MATERIAL STUDIED. 2233, 2599 ex large intestine Bandicota bengalensis. Calcutta, India. B.M. (N.H.) Reg. Nos. 1966.213–252.

 $5 \circ \circ$ ex intestine of 'rats'. Pahang, Malaya. B.M. (N.H.) Reg. Nos. 1932.9.21. 1-4.

MEASUREMENTS (in mm) See Table 2.

The anterior region of the body bears small cervical alae. The head carries three lip-lobes.

Male. There are three mamelons; the post-cloacal papillae are pronounced (fig. II & I2); the spicule is small and tapers to a fine point distally (fig. 22); the gubernaculum is small (fig. I7)); and the tail tapers rapidly just posterior of the post-cloacal papillae and forms a long, thin terminal spike (fig. II).

Female. The vagina is directed posteriorly and the eggs are small (fig. 21).

Discussion. This species was initially described by Yamaguti (1935) as Enterobius muris from female specimens only, but later (1941) he redescribed it as Syphacia muris on examination of both male and female specimens. Baylis (1936) observed that specimens of Syphacia from Rattus rattus in India differed in the size and shape of the eggs from those of S. obvelata and S. stroma. He considered that this later character might prove to be a specific feature of these specimens. Subsequently, Maplestone & Bhaduri (1942) on examination of female specimens recovered from rats (Mus decumanus [= Rattus norvegicus]) in India, describe a new species, S. baylisi, using the size of the eggs to differentiate their species from S. obvelata and S. stroma. They also observe that "... these results confirm Baylis' opinion", suggesting that the two sets of specimens are conspecific.

Roman (1951) considers that S. ratti, which he described earlier (Roman, 1945), is on further examination a synonym of S. baylisi. He considers, however, that S. baylisi appears to be distinguishable from S. muris by the larger body-size and by the position of the vulva. Hussey (1957) compared specimens of S. obvelata and S. muris from experimental hosts and concluded that the two species are readily distinguishable. She agrees with Tiner (1948) that S. venteli and S. muris are synonymous.

A comparison of the descriptions and measurements given by Maplestone & Bhaduri (1942), Roman (1945 & 1951) for S. baylisi and by Travassos (1937) for S. venteli, with those given by Yamaguti (1935 & 1941) and the present material, shows that all these specimens agree in sufficient detail to warrant their reference to S. muris.

S. muris is distinct in the structure of the head: the male in the number of mamelons, in the pronounced post-cloacal papillae, in the size and shape of both the spicule and the gubernaculum, and in the length of the tail; the female in the length of the oesophagus, in the position of the vulva and in the size of the eggs.

Syphacia peromysci Harkema, 1936

MATERIAL STUDIED. 433,799 ex Peromyscus maniculatus. Utah, U.S.A.

MEASUREMENTS. The material available is insufficient to contribute any significant information to that already available.

The head carries three pronounced lip-lobes (Pl. 1, figs. C & D).

Male. There are three ventral mamelons (Pl. 4, fig. A), each one having approximately five or six, small papilla-like structures lying in rows between the strictions (Pl. 5, fig. D) and the structure of the gubernaculum is similar to that of S. emilromani.

DISCUSSION. Harkema (1936) separates this species from *S. obvelata* by its smaller size, by having projecting mamelons and by the size of the eggs. Kruidenier et al. (1961) consider it to be a valid species and distinguish it from *S. samorodini* by the possession of cervical papillae, by the position of the vulva, by the strength and position of the vagina and by the size of the eggs.

This species is similar to S. samorodini as shown by the comparative measurements of Kruidenier et al. (1961). Nevertheless, the difference in the position of the vulva may prove to be sufficient to separate S. peromysci and S. samorodini and both are here provisionally accepted as valid.

Syphacia citelli Tiner & Rausch, 1950

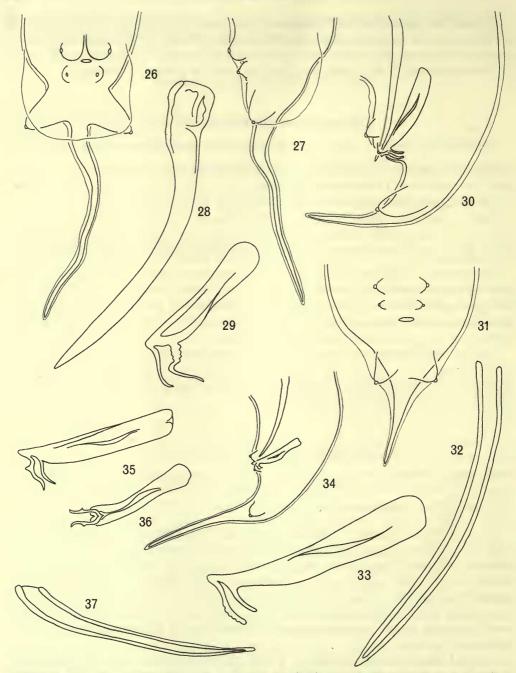
Material studied. 633, 399 (juvenile) ex caecum *Citellus variegatus*. Utah, U.S.A.

2 & 3, 4 \mathcal{P} ex Citellus variegatus, Utah, U.S.A.

Measurements (in mm). Males (from the first listed material only): body-length 2.81, 2.82, 2.89, 3.01, 3.12, 3.16; body-breath 0.236, 0.252, 0.247, 0.272, 0.327, 0.398; diameter of head 0.043, 0.034, 0.045, 0.047, 0.044, 0.047; oesophagus length 0.408, 0.445, 0.434, 0.508, 0.477, 0.437; distance of mamelons from cloacal opening,—posterior 0.78, 0.69, 0.83, 0.87, 0.82, 0.79; —anterior 1.18, 1.18, 1.37, 1.62, 1.20, 1.13; length of spicule 0.092, 0.101, 0.100, 0.098, 0.104, 0.090; length of gubernaculum 0.025, 0.028, 0.029, 0.030, 0.032, 0.029; length of tail 0.189, 0.198, 0.191, 0.212, 0.177, 0.199.

Cervical alae appear to be absent. The head is not pronounced, and the lips appear to have a cuticular thickening (Pl. 2, fig. A). An inner circle of six circumoral papillae is present.

Male. There are two mamelons; the small papilla-like structures seem to be arranged in rows of seven or eight between the transverse striations of the mamelons



Figs. 26-37. 26. Ventral view of male tail, S. citelli 27. Lateral view of male tail, S. citelli 28. Lateral view of spicule, S. citelli 29. Lateral view of gubernaculum, S. citelli 30. Lateral view of male tail, S. pallaryi 31. Ventral view of male tail, S. pallaryi 32. Lateral view of spicule, S. pallaryi 33. Lateral view of gubernaculum, S. pallaryi 34. Lateral view of male tail, S. transafricana 35. Lateral view of gubernaculum, S. transafricana 36. Ventral view of gubernaculum, S. transafricana 37. Lateral view of spicule, S. transafricana.

(Pl. 5, fig. B); the post-cloacal papillae are pronounced (figs. 26 & 27); the spicule is curved distally (fig. 28); the gubernaculum is complex (fig. 29); the tail tapers rapidly posterior to the post-cloacal papillae to form a long, thin, terminal spike (fig. 26).

Female. Although these specimens are almost ten times longer than those of

S. obvelata the eggs are of a similar size; the tail tapers gradually to a point.

DISCUSSION. This species has hitherto been known only from the description by Tiner & Rausch (1950) who merely figured an *en face* diagram of the head. It appears in both sexes to be distinct in the structure of the head; the male in the size of the spicule, in the size and shape of the gubernaculum, in the structure of the cloacal region, in the size and shape of the tail and in the number and structure of the mamelons.

Syphacia pallaryi (Seurat, 1915)

Material studied. 433, 2599 ex caecum of Xerus getulus. Agadir, Morocco.

MEASUREMENTS (in mm). See Table 3.

The head bears three, small, triangular lips (Pl. 2, fig. B).

Male. Two mamelons are present; the post-cloacal papillae are pronounced (fig. 30); the spicule is of a medium length (fig. 32); the gubernaculum is characterised by the notches on the distal barb-like structure (fig. 33); the tail tapers rapidly to a short terminal spike (fig. 31).

Female. The vulva is protruded in both gravid and non-gravid specimens; the non-gravid specimens have a brown cement-cap over the vulva (Pl. 3, fig. F); the

musculature of the vagina is pronounced; the eggs are of a medium size.

DISCUSSION. This species was initially described by Seurat (1915). It has since been redescribed once, by Chabaud & Biocca (1955), who compared it with *S. transafricana* from which it may be readily differentiated (see Discussion of *S. transafricana*, below).

Syphacia transafricana Chabaud & Biocca, 1955

MATERIAL STUDIED. 25 & 3, 25 & 9 & ex caecum of Xerus erytropus. Dakar, French West Africa. Paratype-specimens.

MEASUREMENTS (in mm) See Table 3.

The anterior region of the body carries small cervical alae. The head bears three lips, which are reduced in size and appear to have an internal cuticular thickening

(Pl. 2, fig. C).

Male. Two mamelons are present; the post-cloacal papillae are not pronounced (fig. 34); the spicule is of medium size and tapers to a point distally; the gubernaculum is complex and has an additional pair of lateral processes mid-way along the distal barb-like structure (figs. 35 & 36); the tail narrows suddenly at a level with the post-cloacal papillae and has a thin, terminal spike (fig. 34).

Female. The vagina is directed posteriorly and the vulva is not pronounced; the

eggs are of a medium size.

Discussion. This species was initially described by Chabaud & Biocca (1955), who considered that it could be distinguished from S. pallaryi by the shape of the gubernaculum and the cloacal region of the male. Undoubtedly this species is similar to S. pallaryi, but the males may be readily differentiated from each other by the size of the spicule, by the shape and size of the gubernaculum, by the reduced size of the post-cloacal papillae and by the shape of the tail. Female specimens appear to be similar in most features, the protrusion of the vulva in specimens of S. pallaryi examined is not thought to be significant.

Syphacia thompsoni Price, 1928

MATERIAL STUDIED. I 3, $3 \circ \varphi$ ex Glaucomys sabrinus macrotis. Millestone, Jackson County, Wisconsin, U.S.A. B.M. (N.H.) Reg. Nos. 1951.12.14.149–151. I 3, $2 \circ \varphi$ ex Glaucomys sabrinus. Utah, U.S.A.

MEASUREMENTS (in mm). Only the first listed specimens have been measured. *Male*. Body length 2·66; body-breath 0·141; diameter of head 0·047; oesophagus length 0·387; distance of mamelons from cloacal opening,—posterior 0·224,—middle 0·416,—anterior 0·658; length of spicule 0·187; length of gubernaculum 0·103; length of tail 0·312.

Females. Body-length 8·20, 9·07, 9·53; body-breadth 0·313, 0·311, 0·378; diameter of head 0·064, 0·061, 0·068; oesophagus length 0·521, 0·502, 0·551; distance of vulva from anterior end of body 1·39, 1·46, 1·37; length of tail 2·02, 2·29, 2·58.

The anterior end of the body has distinct cervical alae, which arise just behind the head and terminate approximately on a level with the middle of the oesophagus. The

head bears three lips separated by interlabial grooves (Pl. 1, figs. E & F).

Male. Three mamelons are present; the post-cloacal papillae are pronounced (fig. 38); the spicule is slightly curved and tapers rapidly to a point distally (fig. 38); the gubernaculum has the typical shape, but it is notched on the distal part, similar to that found in S. emilromani; the tail tapers rapidly posterior to the post-cloacal papillae to form a long, thin, terminal spike.

Female. None of the specimens examined are gravid; the tail is long and tapers

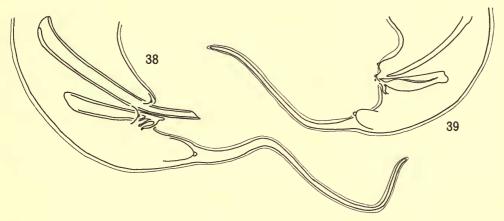
gradually to a fine point.

DISCUSSION. This species has been described previously from Glaucomys v. volvans by Price (1928) and from Sciurus vulgaris and Sciurotamias davidianus by Li (1933). In addition, Tiner & Rausch (1949) report the discovery of this species from the caecum of Tamiasciurus hudsonicus. However, as these specimens consisted of thirty-two males, but no females, they suggest that this infection is in an unnatural host.

The specimens described here agree in most respects with those previously described, although there appears to be an error in the length of the female tail as reported in the table of measurements by Li (1933). The author does not agree with the observation made by Schmidt & Kuntz (1968), that "... the specimens described

as *S. thompsoni* by Li (1933) represent an unnamed species", because the only differences between the two batches of material are in some measurements, whilst the morphological descriptions are very similar. It is possible that these differences in measurements may prove to be significant, but this can only be established by a comparison of the two sets of specimens.

This species is distinct in the structure of the head and in overall size; in the male, the size and shape of the spicule and gubernaculum, the size of the cloacal papillae and the shape of the tail are its diagnostic features.



Figs. 38-39. 38. Lateral view of male tail, S. thompsoni. 39. Lateral view of male tail, S. pearsei.

Syphacia pearsei Baylis, 1928

MATERIAL STUDIED. 3333, 499 ex caecum of *Heliosciurus isabellinus*. Ase, Nigeria. B.M. (N.H.) Reg. Nos. 1929.1.24.22-24. Cotype and paratype specimens. The anterior end of the body has cervical alae. The head bears three lips, each of which is separated by an interlabial groove (fig. 8).

Male. Two mamelons are present; the spicule is of medium length, slightly curved and pointed distally; the gubernaculum is complex; the tail is long in the form of a slender terminal spike (fig. 39).

Female. The tail is long and tapers to a fine point.

DISCUSSION. This species has been described only once previously, from *Heliosciurus isabellinus*, by Baylis (1928). There appears to be nothing to add to the description of this species, except to remark on the structure of the head. The specimens of *S. pearsei* are equally preserved in spirit or as permanent slides, the former are in insufficient numbers to enable an *en face* examination, whilst the latter have unfortunately deteriorated and are not suitable for manipulation. Nevertheless, it appears that the structure of the head is similar to that of *S. thompsoni*, compare (figs. 7 & 8.)

This species is distinct in the structure of the head; the male is distinctive in the size and shape of the spicule and of the gubernaculum, and in the form of the tail.

Syphacia eutamii Tiner, 1948

MATERIAL STUDIED. 233, 599 ex caecum Eutamias minimus pictus. Deep Creek Mts., Utah, U.S.A.

DISCUSSION. This species has already been adequately described by Tiner (1948). The additional observations reported here are those made possible by using the scanning electron microscope.

The head bears three lips, each of which is supported by a separate cuticular thickening. These thickenings are in the shape of the figure eight cut vertically in half, the middle arm of which is lengthened to connect with the apical region of each lip (Pl. 3, figs. A & B). An inner ring of six circumoral papillae is present.

The cuticle appears to have small vertical striations in addition to the typical transverse striations (Pl. 5, fig. A). In male specimens there are numerous, small, papilla-like structures (Pl. 4, fig. C) lying between the striations of the two ventral mamelons.

This species is distinct in the structure of the head; the male is specific in the structure of the spicule and the gubernaculum, in the structure of the cloacal region, in the size of the tail and in the number and structure of the mamelons.

ACKNOWLEDGEMENTS

I am most grateful to Mr. S. Prudhoe, British Museum (Natural History), for his advice and criticism. I would also like to thank Prof. A. G. Chabaud of the Museum National d'Histoire Naturelle, Paris, and Dr. A. W. Grundmann of the University of Utah, U.S.A., for the loan of material.

TABLE I

Ratios and standard deviations for Syphacia obvelata, S. emilromani, S. muris and S. stroma.

The range and values for each ratio is shown by the bracketed figures.

| | S. obvelata | S. emilromani | S. muris | S. stroma |
|---------|--------------|-----------------|--------------|-------------|
| males | | | | |
| b | 5.96 ± 0.43 | 6.58 ± 0.34 | 7.31 ± 0.54 | 5.24 ± 0.39 |
| C | 9·10 ± 0·93 | 9.01 ± 0.62 | 6.07 ± 0.47 | 9.28 ± 1.36 |
| n | II | 25 | 22 | II |
| females | | | | |
| b | 12.93 ± 0.87 | 9.72 ± 0.57 | 11.28 ± 1.26 | 8·16 ± 0·94 |
| С | 6.03 ± 0.47 | 6·47 ± 0·49 | 6.59 ± 0.42 | 6.93 ± 1.11 |
| V | 12·7 ± 1·27 | 22·I ± I·24 | 23.9 ± 1.72 | 23·3 ± 2·27 |
| n | 25 | 25 | 25 | 25 |

b = length / length of oesophagus from anterior end; c = length / length of tail; V = length / distance of vulva from anterior end; n = number of specimens.

TABLE 2

Measurements of Syphacia obvelata, S. emilromani, S. muris and S. stroma. (a) males (b) females. All measurements in mm.

| | S. stroma | 0.95 -1.69 (1.22) | 0.068-0.153 (0.113) | 0.027-0.044 (0.035) | | 0.120-0.166 (0.139) | 0.242-0.303 (0.270) | 0.360-0.462 (0.401) | 0.071-0.084 (0.078) | 0.029-0.044 (0.036) | | | | 2.12 -3.77 (2.94) | 7 | 0.041-0.057 (0.051) | | 0.46 -0.89 (0.68) | | 0.36 -0.53 (0.43) | 0.128×0.039 to | 0.148×0.046 | 25 |
|-----|---------------|-------------------|---------------------|---------------------|-------------------|----------------------|----------------------|---------------------|---------------------|---------------------|----------------|---------------------|-----|-------------------|--------------|---------------------|-------------------|------------------------|----------------------|--------------------|-------------------|-------------|---------------------|
| | ris | (1.42) | (0.092) | (0.033) | (0.193) | (0.148) | (0.302) | (0.427) | (0.053) | (0.025) | (0.235) | | | (3.72) | (0.288) | (0.047) | (0.320) | (68.0) | | (0.26) | to | | |
| | S. muris | 98.1- 06.0 | 0.052-0.148 | 0.023-0.045 | 0.137-0.242 | 0.112-0.195 | 0.230-0.370 | 0.310-0.508 | 0.045-0.058 | 0.018-0.029 | 0.135-0.308 | 22 | | 2.72 -4.34 | 0.181-0.357 | 0.036-0.056 | 0.249-0.416 | 0.56 -1.08 | | 0.40 -0.66 (0.56) | 0.066×0.030 to | 0.091×0.043 | 25 |
| | nani | (2.15) | (0.121) | (0.040) | (0.327) | (0.230) | (0.250) | (0.781) | (080.0) | (0.030) | (0.217) | | | (4.37) | (0.270) | (0.021) | (0.420) | (96.0) | | (89.0) | to | | |
| (a) | S. emilromani | 1.82 -2.50 | 0.099-0.145 | 0.036-0.055 | 0.301-0.374 | 0.161-0.383 | 0.387-0.729 | 0.610-1.056 | 0.074-0.091 | 0.035-0.043 | 0.199-0.242 | 25 | (q) | 3.61 -4.89 | 0.212-0.352 | 0.044-0.058 | 0.364-0.497 | 0.82 -1.06 | | 0.53 -0.82 (0.68) | 0.068 × 0.034 to | 0.085×0.038 | 25 |
| | ata | (1.35) | (0.146) | (0.050) | (0.226) | (0.178) | (0.326) | (0.462) | (8.00) | (0.034) | (0.149) | | | (4.69) | (0.316) | (0.046) | (0.362) | (0.20) | | (0.78) | ę | | |
| | S. obvelata | 1.13 -1.61 | 0.131-0.172 | 0.021-0.034 | 0.188-0.249 | 0.132-0.209 | 0.268-0.374 | 0.388-0.522 | 680-0-890-0 | 0.026-0.039 | 0.122-0.172 | II | | 3.72 -5.61 | 0.234-0.372 | 0.036-0.050 | 0.329-0.431 | 0.45 -0.74 | | (84.0) 68.0- 89.0 | 0.099 × 0.036 to | 0.118×0.041 | 25 |
| | | | | | | i. | 5. | 33 | | | | | | | | | | | | | | | |
| | | Body-length | Body-breadth | Diameter of head | Oesophagus length | Distance of mamelons | from cloacal opening | | Spicule-length | Gubernaculum-length | Length of tail | Number of specimens | | Body-length | Body-breadth | Diameter of head | Oesophagus length | Distance of vulva from | anterior end of body | Length of tail | Range of egg size | | Number of specimens |

TABLE 3

Measurements of Syphacia montana, S. pallaryi and S. transafricana. (a) males (b) females. All measurements in mm.

(a)

| S. transafricana $1.32 - 1.63$ (1.48) | 0.084-0.119 (0.100) | | 0.166-0.179 (0.173) 0.324-0.360 (0.347) | 0.065-0.077 (0.072) | 0.037-0.048 (0.041) 0.088-0.116 (0.102) | 25 | | 2·27 -3·09 (2·76) 0·151-0·302 (0·208) | 0.026-0.036 (0.031) | 0·333-0·512 (0·373) 0·40 -0·74 (0·59) | | 0.065 X 0.026 to | 0.087×0.038 | 25 |
|--|----------------------------------|-------------------|---|---|--|---------------------|-----|--|---------------------|---|-------------------------------------|-------------------|---------------|---------------------|
| S. pallaryi 1.43 –2·21 (1·78) | 0.139-0.234 (0.175) | | 0.138-0.249 (0.211) 0.278-0.604 (0.486) | (201.0) 211.0-101.0 | 0.065-0.069 (0.067) 0.106-0.121 (0.112) | 4 | | 2.90 -3.92 (3.41) 0.228-0.345 (0.301) | | 0.469-0.582 (0.523) | | 0.072 × 0.028 to | 0.091 × 0.033 | 25 |
| S. montana = obvelata $1.33 - 1.77$ (1.54) | 00 10 | | 0.177-0.292 (0.228) 0.385-0.590 (0.439) | 0.413-0.817 (0.569) 0.077-0.083 (0.081) | 0.036-0.041 (0.039) | 5 | (a) | 3.24 -4.99 (4.35) 0.172-0.279 (0.234) | | 0.294-0.364 (0.344) | | 0.104 X 0.30 to | 0·122 × 0·047 | 25 |
| Body-length | Body-breadth Diameter of head | Oesophagus length | Distance of mamelons I. from cloacal opening 2. | 3. Spicule-length | Gubernaculum-length Length of tail | Number of specimens | | Body-length Body-breadth | Diameter of head | Oesophagus length Distance of vulva from | anterior end of body Length of tail | Range of egg size | | Number of specimens |

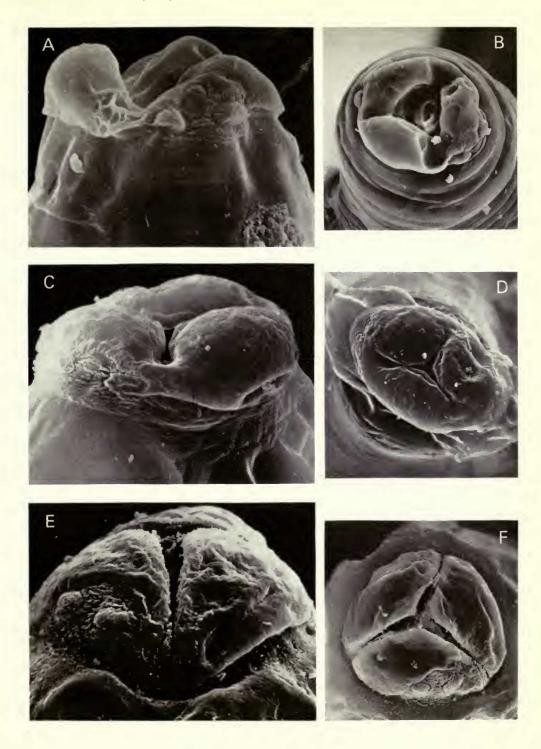
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- A. Dorso-lateral view of head, S. stroma, \times 1,500
- B. En face view of head, S. stroma, lip-lobes slightly distorted, \times 750
- C. Dorso-lateral view of head, S. peromysci, × 1,500
- D. En face view of head, S. peromysci, × 750
- E. Dorso-lateral view of head, S. thompsoni, showing interlabial grooves, X 1,500
- F. En face view of head, S. thompsoni, × 750



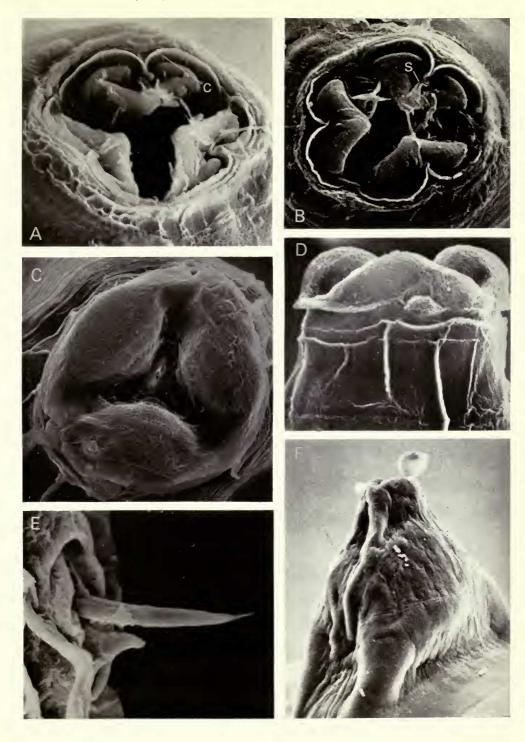
- A. En face view of head, showing cuticular thickening, S. citelli, \times 1,500 B. En face view of head, S. pallaryi, \times 1,500 C. En face view of head, S. transafricana, \times 1,500







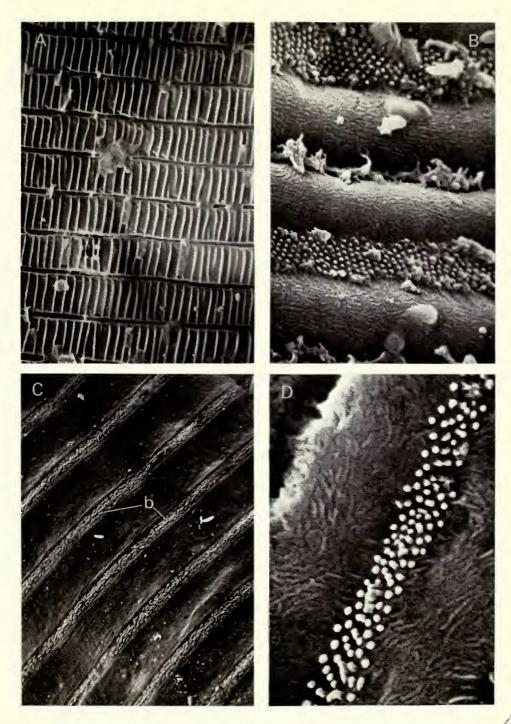
- A. Dorso-lateral view of head, S. eutamii; c, cuticular thickening, × 1,500
- B. En face view of head, S. eutamii; s, supporting septum, \times 1,500
- C. En face view of head, S. emilromani, X 1,500
- D. Dorso-lateral view of head, S. emilromani, × 1,500
- E. Lateral view of spicule projecting from cloacal opening, S. obvelata, × 2,800
- F. Vulva of S. pallaryi, with partly detached cement-cap, cp. \times 1,260



- A. Lateral view of male, S. peromysci, showing three mamelons, m, and lateral line, l, × 140
- B. Anterior mamelon of S. stroma, showing division of transverse ridge into two shallow elevations, × 1,000
- C. Detail of papilla-like structures, S. eutamii, × 12,800
 D. Detail of shallow elevations and papilla-like structures, S. obvelata, × 2,700
 E. Detail of papilla-like structures, S. stroma, × 21,000



- A. Cuticle of S. eutamii, showing transverse striations and small longitudinal ridges, × 2,100
 B. Shallow elevations and papilla-like structures of S. citelli, × 6,900
 C. Cuticle of S. transafricana; b, bacteria lying in the the transverse striations, × 1,140
 D. Detail of papilla-like structures, S. peromysci, × 15,000



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